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MOLECULAR PHYLOGENETIC EVIDENCE FOR THE PARALLEL EVOLUTION OF ROCK ECOMORPHS IN THE NEW ZEALAND ORB-WEAVING SPIDER *WAITKERA WAITAKERENSIS* (FAMILY ULOBORIDAE)

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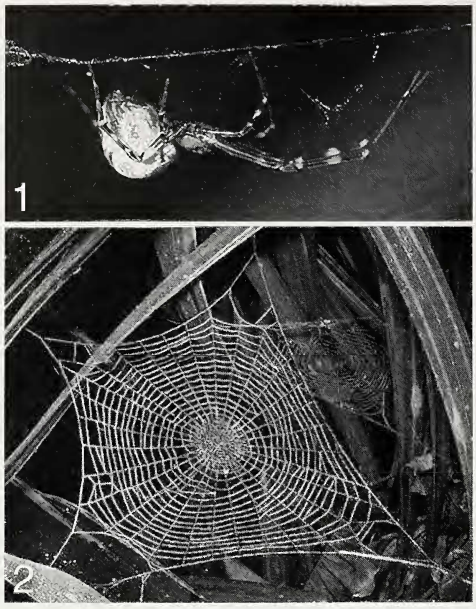
ABSTRACT. The genus *Waitkera* is the only New Zealand representative of the family Uloboridae and is known from a single species, *Waitkera waitakerensis*. This species is found in forests of the North Island, where it constructs orb-webs on understory vegetation. Rock outcrops in the Northland region support populations of *W. waitkerensis* comprised of larger individuals than those found elsewhere on the island, including those in surrounding forests. Parsimony analyses of DNA sequences from the mitochondrial NADH dehydrogenase subunit ND1, using *Siratoba refernes*, another basal uloborid, as an outgroup, did not delineate these rock-dwelling populations as a monophyletic lineage that could be regarded as a distinct species. A TCS analysis leads to the same conclusion, suggesting that rock-dwelling populations represent independently evolved ecotypes. Northland populations of *W. waitakerensis* are phylogenetically basal; indicating that the species' range contracted northward during the Pleistocene and recolonized the remainder of the North Island.

Keywords: Araneae, Uloboridae, phylogeography, ND1 mitochondrial DNA, nested clade analysis

The monotypic genus *Waitkera* (Opell 1979) is New Zealand's only representative of the family Uloboridae. *Waitkera waitakerensis* (Chamberlain 1946) is comprised of small spiders (Fig. 1) that construct horizontal orb-webs in understory vegetation (Fig. 2). Females have a cephalothorax-abdomen length of 4–5 mm and males of 3–4 mm. Adult female mass averages 9 mg (Opell 1999). Evidence of this species can also be found in their peaked, triangular egg sacs (Fig. 3) that are deposited at the edges of their webs. In the Northland region, egg sacs are first produced in early to mid January and spiderlings begin to emerge from them about one month later (Opell unpublished observations). There are few published records of *W. waitakerensis* (Forster 1967; Forster & Forster 1999). However, this species is sometimes the most numerous orb-weaver in a forest (Opell unpublished observations) and I have collected it from localities throughout the North Island (Fig. 4) in kauri-podocarp-hardwood, lowland podocarp-hardwood, and lowland hardwood forests. I did not observe *W. waitakerensis* in beech forests of the Huiarau or Ruahine Ranges, the extent of my searches in this habitat.

Pleistocene glaciation affected populations of New Zealand's terrestrial arthropods (Trewick 2001) and is likely to have impacted *W. waitakerensis*. The restriction of this species to New Zealand's North Island suggests that during the Pleistocene (New Zealand Wanganui series) this, and perhaps other species of the genus, may have been eliminated from the South Island. In fact, during the Pleistocene, it is probable that the range of *W. waitakerensis* contracted to the warm climate forests that persisted only in the Northland region (Suggate 1978; Thornton 1985). Other events may have contributed to the extirpation of these spiders. The eruption of the North Island's Taupo Volcano 20,000 years ago (Thornton 1985) and again about 1855 years ago (Wilson & Walker 1985) formed deep ash fields that extended for hundreds of kilometers (Fig. 4). These eruptions have impacted populations of other species (McDowall 1996; Morgan-Richards et al. 2000, 2001) and would have been catastrophic for orb-weaving spiders living in the central portion of the North Island.

It is possible that additional species of *Waitkera* survived these events by occupying refugia (Pielou 1991; Pfenninger et al. 2003; Trewick 2001). A likely place for these refu-



Figures 1–2.—*Waitkera waitakerensis*: 1. Adult female on web; 2. Horizontal orb-webs.

Figure 3.—Egg sacs of *W. waitakerensis* attached at the edge of an orb-web.

gia is the Northland region, which has been collected less thoroughly than most regions of New Zealand and in which cryptic species have been discovered (Gleeson et al. 1999). In this region I discovered a population of *Waitkera* that appeared to represent such a relict species. These spiders were living in the cool, shaded rock crevices of the Waro Limestone Reserve, near Hikurangi (Fig. 5, population 4; Hawley 1981). These crevices extended deep into this karstic area, as evidenced by the cool air coming from many of them. At this site, the spiders, their webs, and their egg sacs were conspicuously larger than those of forest-dwelling populations elsewhere on the North Island, including those in the vicinity of this reserve.

The Waro rock formation is the textbook example of an extensive formation of soft Oligocene limestone that, after being uplifted by the collision the Indo-Australian and Pacific plates, slid westward to form the surface of the eastern one-third of the Northland region (Fig. 5; Suggate 1978; Thornton 1985). I found populations of the larger, rock-dwelling *Waitkera* in outcrops of this formation at three additional sites: Waiomio Glow Worm Cave near Kawakawa, Abbey Caves east of Whangarei, and Waipu Caves south of Whangarei (Fig. 5, populations 19, 6, and 8, respectively).

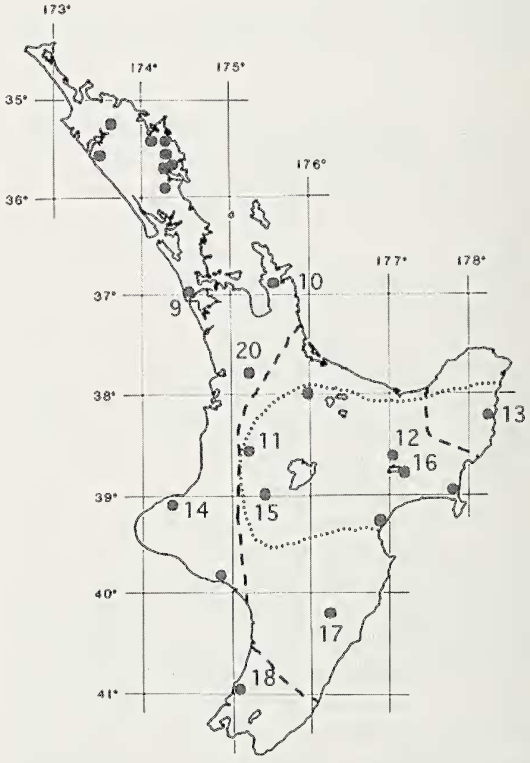


Figure 4.—Sites at which *W. waitakerensis* was observed by B. Opell. Numbers refer to localities given in Table 1. Heavy dashed lines denote the boundaries of ash deposited by the eruption of the Taupo Volcano about 20,000 years ago and light dashed lines for an eruption about 1855 years ago (Thornton 1985; Wilson & Walker 1985).

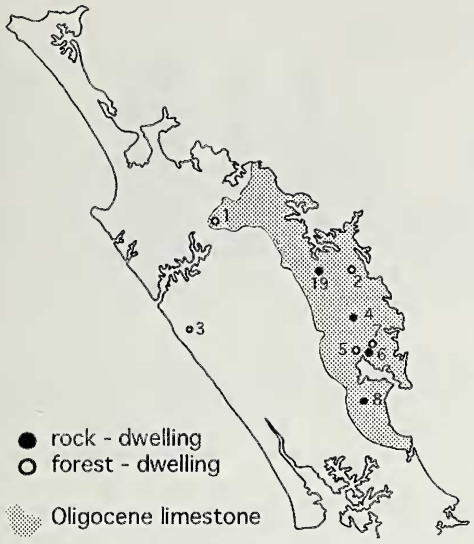


Figure 5.—Oligocene limestone distribution in the Northland and localities of rock-dwelling and forest-dwelling populations in this region. Numbers refer to localities given in Table 1.

There, appears to be no mechanism for direct gene flow between these rock-dwelling populations. A distance of about 12 km separates the closest rock-dwelling sites. *W. waitakerensis* does not appear to be troglophilic. I did not find these spiders either at the entrances of Waipoua Cave, Abbey Caves, or Waipu Cave or in the first 20 m of these caves.

Ecological and morphological evidence suggest that the rock-dwelling *Waitkera* populations may represent one or more undescribed species. However, more convincing support for this hypothesis would come from documentation that these populations form a monophyletic lineage. In this case, such evidence can best come from a molecular comparison of these populations. Therefore, I examined the relationships among *Waitkera* populations using DNA sequences of the mitochondrial NADH dehydrogenase subunit ND1. This rapidly evolving gene has been used successfully to reconstruct the phylogenies and examine the population structure of other closely related spider species (Hedin 1997a, 1997b; Hedin & Maddison 2001; Masta & Maddison 2002).

METHODS

Morphology.—To document the morphological differences among populations, I used a Wild M8 dissecting microscope equipped with an ocular reticle to measure the first femur lengths of ten alcohol-preserved adult female specimens from each of nine forest-dwelling populations and four rock-dwelling populations. I compared the mean femur lengths of these fourteen populations using a Ryan-Einot-Gabriel-Welsch Multiple Range Test (alpha = 0.05) (Day & Quinn 1989) performed with the SAS statistical program (Cary, North Carolina) run on a personal computer. *W. waitakerensis* females have a large, spherical median spermatheca (Opell 1979). To examine differences in reproductive morphology relative to somatic features, I measured the carapace lengths and spermathecal widths of 24 forest-dwelling females from localities throughout the North Island and of five females from each of the four rock-dwelling populations. Carapace length was measured under a dissecting microscope. Spermathecal width was measured under a compound microscope from a genital region that had been removed, cleared in clove oil, and temporarily mounted on a microscope slide under a cover slip. Voucher specimens from each of these populations have been deposited in collections of Landcare Research, Auckland and the Otago Museum, Dunedin, New Zealand.

Molecular.—The molecular study included 40 specimens from 18 populations: 3 Northland rock populations, 5 Northland forest populations, 2 populations from the north central region of the island, and 8 populations from the central and southern regions of the island (Table 1; Fig. 4). I used two specimens of *Siratoba referens* (Muma & Gertsch 1964) from the vicinity of Portal, Cochise County, Arizona as an outgroup for *W. waitakerensis*. This was the most basal uloborid (Coddington 1990) for which I could obtain DNA. Voucher specimens from each of these populations have been deposited in the collections of the Otago Museum, Dunedin, New Zealand.

I extracted DNA from these alcohol-preserved specimens using a Puregene DNA isolation kit from Gentra Systems, Inc. and used PCR to amplify the double-stranded ND1 subunit of mitochondrial NADH dehydrogenase, employing the primers and thermocycler parameters described by Hedin (1997a). For each specimen, I obtained the sequences of both DNA strands using cycle sequencing, Biosystems' Big Dye Terminator™ chemistry, and a 3100 genetic analyzer instrumentation from Ap-

Table 1.—Localities and their haplotypes. Locality numbers correspond to sites shown in Figures 4 and 5, the values plotted in Figures 6 and 7, and the distribution of haplotypes depicted in Figure 8. Specimens from localities 19 and 20 were not included in phylogenetic analyses.

Locality numbers	Locality	°Latitude	Longitude	Habitat	Individuals per haplotype
1	Mangamuka Bridge, Omahuta State Forest	−35.2273	173.5880	forest	1 H1
2	Russell State Forest, near Punaruku Road	−35.3799	174.2438	forest	1 H1, 1H2
3	Waipoua Forest	−35.6164	173.5405	forest	1 H1, 1 H7, 1 H8
4	Hikurangi, Waro Limestone Scenic Reserve	−35.5837	174.2864	rocks	3 H1
5	Whangarei, Coronation Scenic Reserve	−35.7303	174.3093	forest	2 H1, 1 H6
6	Whangarei, Abbey Caves Reserve	−35.7112	174.3574	rocks	3 H1
7	Whangarei, Reed Memorial Kauri Reserve	−35.7071	174.3207	forest	1 H4
8	Waipu Caves	−35.9396	174.3463	rocks	2 H1, 1 H3, 1 H9
9	Karekare, McReady Paddock	−36.9904	174.4675	forest	1 H9, 1 H16
10	Manaia, Mahakirau Reserve	−36.8551	175.6121	forest	1 H10, 1 H11
11	Mapiu, Aratoro Scenic Reserve	−38.3295	175.1712	forest	2 H12
12	Te Whaiti	−38.5873	176.7816	forest	2 H9
13	Anaura Bay, walkway	−38.2378	178.3298	forest	2 H12
14	New Plymouth, Meeting of the Waters Scenic Reserve	−39.1416	174.1487	forest	1 H12, 1 H15
15	Owhango, Ohinetonga Scenic Reserve	−38.9916	175.3673	forest	2 H14
16	Urewera National Park, L., Waikaremoana, Lou's Lookout	−38.7373	177.1030	rocks	1 H12, 1 H13
17	Dannevirke, Ngapaeruru Scenic Reserve	−40.2616	176.2328	forest	2 H12
18	Paekakariki, Kapiti Borough Council Reserve Walkway	−40.9844	174.9441	forest	2 H12
19	Waiomio Glow Worm Cave near Kawakawa	−35.4144	174.0646	rock	
20	Hamilton	−37.7815	175.2817	forest	

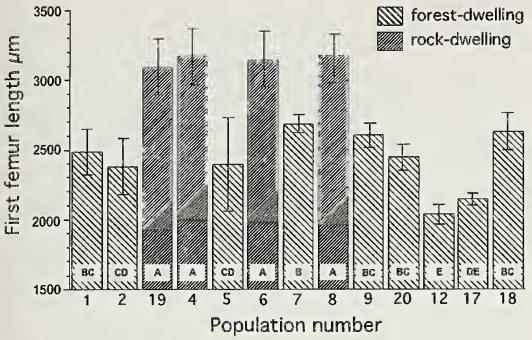


Figure 6.—Histogram of adult female first femur lengths of rock-dwelling and forest-dwelling populations, arranged (from left to right) in a north to south order. Population numbers refer to localities shown in Figures 4 and 5 and described in Table 1. The sample size for each population is 10 individuals. Error bars denote ± 1 standard deviation. Letters within histogram bars denote the ranking of mean values assigned by a Ryan-Einot-Gabriel-Welsch Multiple Range Test (alpha = 0.05) (Day & Quinn 1989).

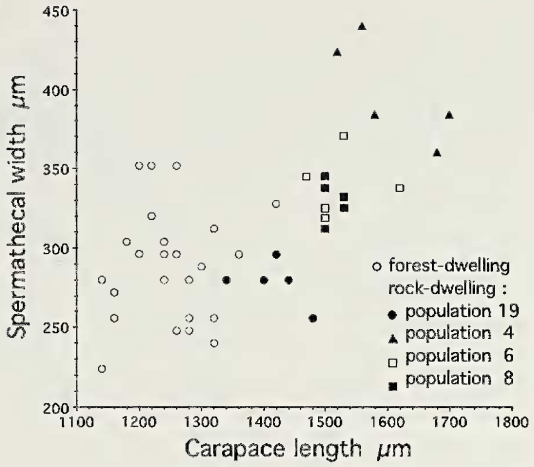


Figure 7.—Plot of adult female *W. waitakerensis* spermatheca width and carapace length. Population numbers refer to localities shown in Figures 4 and 5 and described in Table 1.

plied Biosystems. Each electropherogram was edited with the EditView program and then aligned with its complementary sequence. Discrepancies were reedited and new sequencing reactions were run when required. Clustal V (Higgins et al. 1996), as implemented by DNA Star, was used to align sequences.

Maximum parsimony and maximum likelihood analyses were implemented with Paup* 4.0b10 (Swofford 1998). Modeltest 3.6 (Posada & Crandall 1998) was run using the likelihood scores generated by PAUP under the "longfmt=yes" option of the Lscores command to determine the preferred maximum likelihood model. The selected model and its values were entered into the maximum likelihood settings of PAUP. The TCS program (Clement et al. 2000) was used to perform Templeton, Crandall, Sing analysis (statistical parsimony analysis; Crandall et al. 1994; Templeton 1998; Templeton et al. 1992). The GeoDis 2.2 program (1999–2004 David Posada) and its June 2004 inference key (Templeton et al. 1995; Posada & Templeton 2000) were used to perform a nested haplotype analysis (Templeton et al. 1987; Crandall 1994, 1996).

RESULTS

Morphology.—Spiders from the four rock-dwelling populations were larger than those from the ten forest-dwelling populations (Fig. 6). These size differences are also reflected in male and female genitalia, although there are no qualitative shape differences, perhaps due to the very simple nature of the genitalia (Opell 1979). As Figure 7 illustrates, rock-dwelling females have larger spermathecae than forest-dwellers. This may simply be a reflection of the larger body size of rock-dwellers, although recent molecular studies of millipedes and spiders show that genitalic morphology can underestimate species diversity (e.g., Bond & Sierwald 2002; Bond et al. 2001). It is interesting to note that spermathecae of three of the four rock-dwelling populations are as distinct from one another as they are from the forest-dwelling populations. This could suggest that even greater diversity is represented among the rock-dwellers or that these populations exhibit more phenotypic plasticity than do forest-dwelling populations.

Molecular analysis.—After uncertain terminal DNA regions were eliminated, 412 base pairs were available for analysis. Three insertions in each *W. waitakerensis* sequence were necessary to align the DNA of this species with that of *S. refernes*. No additional insertions or deletions were necessary. Sequences of both *S. refernes* specimens were identical. Sixteen DNA haplotypes with a mean uncorrected (p) distance of 0.94% (range 0.24–1.71%) were represented by the 40 *W. waitakerensis* specimens (Table 1). The distance between *W. waitakerensis* haplotypes and *S.*

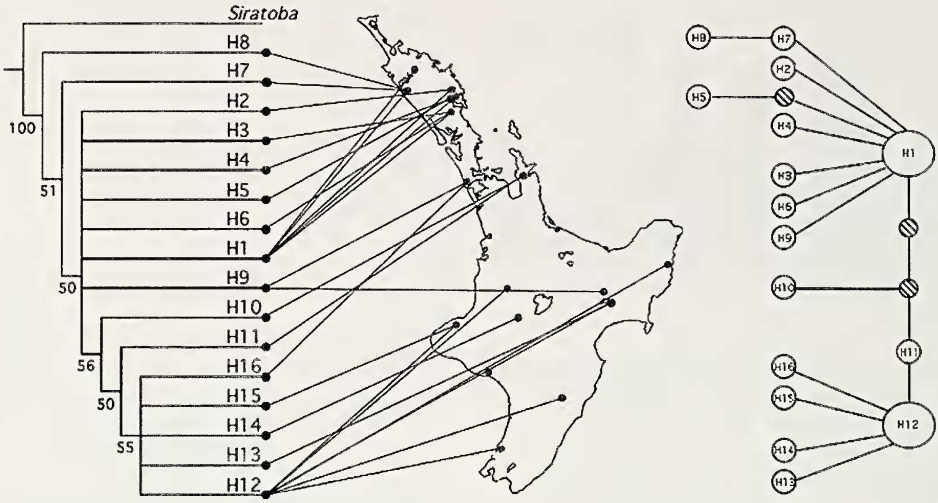


Figure 8.—Parsimony analysis of 16 *W. waitakerensis* ND1 haplotypes run with *S. referens* as an outgroup and mapped onto localities (left) and statistical parsimony (TCS) network of these haplotypes (right). Parsimony analysis is the single tree from a branch and bound search, CI = 0.9846, RI = 0.9231, number of informative characters = 116 (6 within *W. waitakerensis*), 50% majority-rule consensus bootstrap values from a 2000-replicate analysis. In the TCS network open circles represent the haplotypes and cross-hatched circles inferred missing haplotypes. Each line connecting a haplotype represents a single change in one base pair.

referens was 27.6–28.3%. GenBank accession numbers: Siratoba = DQ026788, H1 = AY974175, H2 = AY974176, H3 = AY974177, H4 = AY974178, H5 = AY974179, H6 = AY974180, H7 = AY974181, H8 = AY974182, H9 = AY974183, H10 = AY974184, H11 = AY974185, H12 = AY974186, H13 = AY974187, H14 = AY974188, H15 = AY974189, H16 = AY974190.

Maximum parsimony analysis (branch and bound search) produced a single tree (Fig. 8). Modeltest selected a HKY model and provided the following values used in PAUP's likelihood settings: Ti/tv ratio = 2.6311, empirical base frequencies, among-site rate variation = 0, variable sites = equal rates for all sites, maximum number of branch-length smoothing passes = 20, parameterization for clock model = standard, starting branch lengths for non-clock models = least squares method, Jukes-Cantor. A heuristic search produced a single tree (-Ln likelihood = 994.95) that was identical to that shown in Figure 8. An attempted branch and bound search was terminated after four days of computing.

Parsimony analysis (Fig. 8) roots the tree at two haplotypes (H7 & H8) from Waipoua Forest (locality 3) in the west of the Northland. Relationships among the remaining Northland haplotypes (H1–6 & H9) are not resolved, providing no support for the hypothesis that rock-dwelling populations constitute a distinct lineage. Furthermore, individuals from the three included rocky sites share haplotype H1 with individuals from Northland forest sites. Two Coromandel Peninsula haplotypes (H10–11) lie at the base of a clade that is sister to the unresolved northland haplotypes and terminates in five unresolved central and southern haplotypes (H12–16). The only two haplotypes not explained by a strict cladogram base-to-tip = north-to-south pattern are H9 and H16. H9 is represented both at locality 9, which is consistent with the general pattern, but also at locality 12, a more southern site. H16 is represented at locality 9, a more northern locality than those occupied by the four other members of its unresolved, otherwise southern clade.

Siratoba referens is too distantly related to *W. waitakerensis* to be included in the 95% confidence limits of the statistical parsimony network (Fig. 8). However, if this network is rooted at haplotype H8, its pattern is identical to that of the parsimony analysis. A nested haplotype analysis of geographical distances based on this network (Fig. 9) and distribution

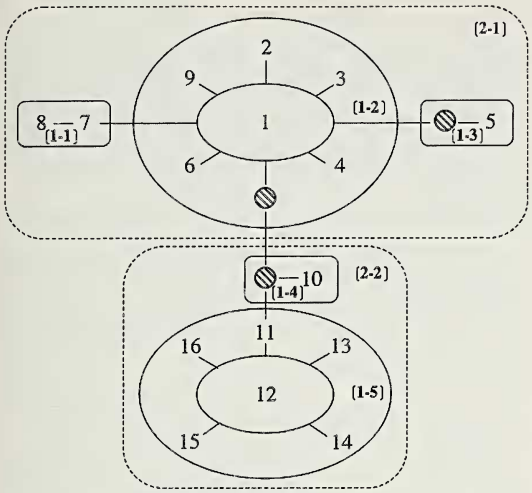


Figure 9.—Haplotype network arranged in hierarchical format for nested haplotype analysis of geographical distances. Numbers within brackets identify the nested clades. Other numbers identify the haplotypes, shown in Fig. 8 and Table 1.

data given in Table 1 was inconclusive. It was unable to determine if the current distribution of *W. waitakerensis* is explained by past fragmentation of a more inclusive distribution, by continuous range expansion, by long distance dispersal, or by combinations of these events. Exact contingency tests for all subclades were insignificant ($X^2 > 7.98$, $P > 0.16$). The exact contingency test for the total cladogram was significant ($X^2 = 37.95$, $P < 0.001$). For this clade (comprised of subclades 2–1 and 2–2) the inference key led through the following couplets: 1, 19, 20 (here, I considered sampling adequate to answer "yes"; however, an answer of "no" leads to the conclusion "inadequate geographic sampling"), and 2, where the conclusion is "tip/interior status can not be determined—inconclusive outcome". This GeoDis analysis placed the geographic center of clade 2–1 in the Northland, just north of Whangarei (between sites 4, 5, and 7) and the geographic center of clade 2–2 northwest of Lake Taupo (just east of site 11).

DISCUSSION

Phylogenetic analyses offer no support for the hypothesis that the rock-dwelling populations of large-bodied *W. waitakerensis* represent a monophyletic lineage that might be considered a species. Some of the individuals from each of these populations share a haplotype with individuals from forest populations. Two unique haplotypes were included in one of the rock-dwelling populations, but these were no more divergent than other unique haplotypes found among Northland forest-dwellers. Thus, rock-dwelling populations appear to represent an ecotype that has arisen multiple times. These populations of *W. waitakerensis* may represent lineages that have recently adapted to karstic areas and have had insufficient time to diverge genetically. As such, they may represent a group of incipient or cryptic species. ND1 DNA may not have diverged rapidly enough to serve as an appropriate genetic marker and other genes might better delineate individuals from rock-dwelling populations. Adult rock-dwelling and forest-dwelling populations do not appear to be temporally isolated, although their microhabitats tend to isolate them physically. Genitalic size differences may also limit gene flow between rock and forest populations, but the simple genitalia of *W. waitakerensis* (females are functionally haplogyne; Opell 1979) may minimize the difficulty of mating by individuals of dissimilar sizes.

The larger size of rock-dwelling spiders in the Northland does not initially appear to conform to intraspecific size clines that characterize many terrestrial arthropods with univoltine life cycle. Larger individuals are typically found in warmer regions at the lower latitudes or lower elevations of a species' range (e.g., Masaki 1978; Mousseau & Roff 1989; Orr 1996; Schoener & Janzen 1968; Scott & Dingle 1990). These warmer regions have longer growing seasons that permit individuals to attain larger adult sizes (Mousseau 1997), a pattern that appears to have an underlying genetic component (Huey et al. 2000). These observations suggest that it may be more appropriate to consider rock-dwelling populations of *W. waitakerensis* as living in more thermally stable microhabitats rather than simply in cooler microhabitats. Under this scenario, spiders in karstic microhabitats would be protected from the low and fluctuating spring temperatures experienced by forest-dwellers and, consequently, would have a longer developmental period permitting them to attain a larger adult size than forest-dwellers.

The population structure of *W. waitakerensis* (Fig. 8) is consistent with a contraction of the species' range to the Northland region

during the Pleistocene glaciation. The most basal haplotypes (H7 & H8) are found in the Northland, as are seven haplotypes derived from them. As the climate warmed, this species recolonized the North Island by way of the Coromandel Peninsula (haplotypes H10–11). Access to more direct central and western corridors may have been blocked by extensive volcanic activity in the Auckland area (Suggate 1978; Thornton 1985). However, this corridor later opened, allowing southern migration of haplotype H9 and northern migration of haplotype H16 into the species' type locality in the Waitakere Mountains north of Auckland (locality 9). This species may have ballooned to the Coromandel Peninsula or it may have expanded southward along with warm climate coastal forests. Colonization of the North Island's central and southern regions appears to have been rapid and perhaps recent, given the occurrence of a common haplotype (H12) at six widely separated sites. The spread of *W. waitakerensis* below the 38th parallel may have been halted or set back by the most recent eruption of the Taupo Volcano (Fig. 4; Wilson & Walker 1985) and populations in the southern half of the North Island may be of very recent origin.

The phylogenetic pattern of *W. waitakerensis* may be characteristic of other New Zealand spiders that require a mild climate and have limited dispersal capabilities. If so, this study indicates that the Northland and Coromandel Peninsula regions, though small in area, contain critical elements of New Zealand's biodiversity.

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LITERATURE CITED

Bond, J.E., M.C. Hedin, M.G. Ramirez & B.D. Opell. 2001. Deep molecular divergence in the absence of morphological and ecological change in the Californian coastal dune endemic trapdoor spider *Aptostichus simus*. Molecular Ecology 10: 899–910.

Bond, J.E. & P. Sierwald. 2002. Cryptic speciation in the *Anadenobolus excisus* species complex on the island of Jamaica. Evolution 56:1123–1135.

Chamberlain, G. 1946. Revision of the Araneae of New Zealand (part 2). Bulletin of the Auckland Institute and Museum 3:85–97.

Clement, M., D. Posada & K.A. Crandall. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology 9:1657–1660.

Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496:1–52.

Crandall, K.A. 1994. Intraspecific cladogram estimation: accuracy at higher levels of divergence. Systematic Biology 43:222–235.

Crandall, K.A. 1996. Multiple interespecies transmissions of human and simian T-cell leukemia/lymphoma virus type I sequences. Molecular Biology and Evolution 13:115–131.

Crandall, K.A., A.R. Templeton, & C.F. Sing. 1994. Intraspecific phylogenetics: problems and solutions. Pp. 273–298. *In* Models in Phylogeny Reconstruction (R.W. Scotland, D.J. Siebert & D.M. Williams, eds.). Clarendon Press, Oxford.

Day, R.R. & G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433–463.

Forster, R.R. 1967. The spiders of New Zealand, Part I. Otago Museum Bulletin 1:7–124.

Forster, R.R. & L. Forster. 1999. Spiders of New Zealand and their Worldwide Kin. University of Otago Press, Dunedin, 270 pp.

Gleeson, D.M, R.L.J. Howitt & N. Ling. 1999. Genetic variation, population structure, and cryptic species within the black mudfish, *Neochanna diversus*, an endemic galaxiid from New Zealand. Molecular Ecology 8:47–57.

Hawley, J. 1981. Waro limestone scenic reserve: a concept for future development. Department of Lands and Survey Report, Auckland, 29 pp.

Hedin, M.C. 1997a. Molecular phylogenetics at the population/species interface in cave spiders of the Southern Appalachians (Araneae: Nesticidae: *Nesticus*). Molecular Biology and Evolution 14: 309–324.

Hedin, M.C. 1997b. Speciational history in a diverse clade of habitat-specialized spiders (Araneae: Nesticidae: *Nesticus*): Inferences from geographic-based sampling. Evolution 51:1929–1945.

Hedin, M.C. & W.P. Maddison. 2001. A combined molecular approach to phylogeny of the jumping spider subfamily Dendrophantinae (Araneae: Salticidae). Molecular Phylogenetics and Evolution 18:386–403.

Higgins, D.G., A.J. Bleasby & R. Fuchs. 1996. Clustal V: Improved software for multiple sequence alignment. Computer Applied Bioscience 8:189–191.

Huey, R.B., G.W. Gilchrist, M.L. Carlson, D. Berrigan & L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287:308–309.

Masaki, S. 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. Pp. 72–100. *In* Evolution of Insect Migration and Diapause (H. Dingle, ed.). Springer-Verlag, New York.

Masta, S.E. & W.P. Maddison. 2002. Sexual selection driving diversification in jumping spiders. Proceedings of the National Academy of Science of the USA 99:4442–4447.

McDowall, R.M. 1996. Volcanism and freshwater fish biogeography in the northeastern North Island of New Zealand. Journal of Biogeography 23:139–148.

Morgan-Richards, M, S.A. Trewick & G.P. Wallis. 2000. Characterization of a hybrid zone between two chromosomal races of weta *Hemideina thoracica* following a geologically recent volcanic eruption. Heredity 85:586–592.

Morgan-Richards, M, S.A. Trewick & G.P. Wallis. 2001. Chromosomal races with Pliocene origins: evidence from mtDNA. Heredity 86:303–312.

Mousseau, T.A. 1997. Ectotherms follow the converse to Bergman's rule. Evolution 51:630–632.

Mousseau, T.A. & D.A. Roff. 1989. Adaptation to seasonality in a cricket: patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. Evolution 43:1483–1496.

Muma, M.M. & J.W. Gertsch. 1964. The spider family Uloboridae in North America north of Mexico. American Museum Novitates 2196:1–43.

Opell, B.D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bulletin of the Museum of Comparative Zoology 14:433–549.

Opell, B.D. 1999. Changes in spinning anatomy and thread stickiness associated with the origin of orb-weaving spiders. Biological Journal of the Linnean Society 68:593–612.

Orr, M.R. 1996. Life-history adaptation and reproduction isolation in a grasshopper hybrid zone. Evolution 50:704–716.

Pfenninger, M., D. Posada & F. Magnin. 2003. Evidence for survival of Pleistocene climatic changes in Northern refugia by the land snail *Trochoidea geyeri* (Soós 1926) (Helicellinae, Stylommatophora). BMC Evolutionary Biology 3:1–13.

Pielou, E.C. 1991. After the Ice Age: The Return of Life to Glaciated North America. University of Chicago Press, Chicago, 366 pp.

Posada, D. & K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Posada, D. & A.R. Templeton. 2000]. *GEODIS 2.0 Documentation.* Provo, Utah.

Schoener, T.W. & D.H. Janzen 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. American Naturalist 102:207–224.

Scott, S.M. & H. Dingle. 1990. Developmental programmes and adaptive syndromes in insect life-cycles. Pp. 69–85. *In* Insect Life Cycles: Genetics, Evolution and Co-ordination (F. Gilbert, ed.). Springer-Verlag, New York.

Suggate, R.P., ed. 1978. The Geology of New Zealand, Vols. 1 & 2. E. C. Keating, Government Printer, Wellington. 820 pp.

Swofford, D.L. 1998. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4. Sinauer Associates, Sunderland, Massachusetts.

Templeton, A.R. 1998. Nested clade analysis of phylogeographic data: testing hypotheses about gene flow and population history. Molecular Ecology 7:381–397.

Templeton, A.R., E. Boerwinkle, & C.F. Sing. 1987. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. I. Basic theory and an analysis of alcohol dehydrogenase activity in *Drosophila.* Genetics 117:343–351.

Templeton, A.R., K.A. Crandall, & C.F. Sing. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetics 132:619–633.

Templeton, A.R, E. Routman, & C.A. Phillips. 1995. Separating population structure from population history: a cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum.* Genetics 140:767–782.

Thornton, J. 1985. New Zealand Geology. Reed Books, Auckland, 216 pp.

Trewick, S.A. 2001. Scree weta phylogeography: surviving glaciation and implications for Pleistocene biogeography in New Zealand. New Zealand Journal of Zoology 28:291–298.

Wilson, C.S. & C.P.L. Walker. 1985. The Taupo eruption, New Zealand. I. General aspects. Philosophical Transactions of the Royal Society of London A 314:199–228.

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